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Spring migration of the Siberian Knots *Calidris canutus canutus*: results of a co-operative Wader Study Group project

William J. A. Dick, Theunis Piersma and Peter Prokosch

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In spring 1979 the Wader Study Group organised a co-operative project to study the spring migration of Siberian Knots *Calidris c. canutus* from their west and south African wintering grounds to the breeding grounds in central Siberia. S. African wintering birds migrate via the western seaboard of Africa and Europe. Siberian Knots seem to use only a few staging sites between W. Africa and Siberia. Most birds only use the W. German Wadden Sea. Staging areas of lesser importance are the Tejo Estuary in Portugal, the Vendée coast in France and, probably, the Westerschelde in SW Netherlands. At the latter three sites in early May, birds appear to arrive with lower body weights than in Schleswig-Holstein (W. Germany) at the same time. The migration from W. Germany to central Siberia is most probably made in one flight via the Gulf of Finland. Detailed information on the timing of migration is presented. A model on body weight changes during migration in a fixed time schedule is employed to discuss the energetic constraints on the migration strategy of Siberian Knots.

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1. Introduction

Knots *Calidris canutus* occurring along the western seaboard of Europe and Africa belong to two distinct populations (Dick et al. 1976). Reproduction of Knots is confined to the high arctic; one population breeds on the Taymir Peninsula and Severnaya Zemlya in central Siberia and the other in the north Canadian Arctic and northern Greenland. Roselaar (1983) recently argued that birds from the two breeding populations are morphologically (based on bill and wing length only) sufficiently distinct to consider them as separate subspecies: the nominate subspecies of Siberian breeding Knots *C. c. canutus* and the Nearctic subspecies *C. c. islandica*. (At least one more subspecies, *C. c. rogersi* breeds in the far north-east of Siberia and another, *C. c. rufa*, in the lower North American Arctic). Plumage and ringing studies showed initially that the Nearctic

birds winter in western Europe (Salomonsen 1950–51, Godfrey 1953, Morrison 1975) and Dick et al. (1976) subsequently demonstrated that the relatively longer-billed birds from Siberia winter in north-western and southern Africa. Apparently, there is little overlap in the winter quarters of the two subspecies. Although something was known about the spring migration of the Nearctic population (Prater 1974, Morrison 1975), the spring migration of the supposedly Siberian breeding Knots wintering in Africa was virtually unstudied. These were the reasons behind the organization in spring 1979, through the Wader Study Group (WSG), of an international project to study the spring passage of Siberian Knots (Dick 1978). Preliminary results of this co-operative endeavour were summarized by Dick (1979), and amplified by Håland and Kålås (1980) and Dick et al. (1980).

This paper aims to present and interpret the observa-

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tions on (Siberian) Knot migration collected by numerous observers in 11 countries in spring 1979. Since then, particular progress has been made in studies of the important staging area in the Schleswig-Holstein Wadden Sea (Prokosch 1984, in press). Some of these more recent data have therefore been incorporated.

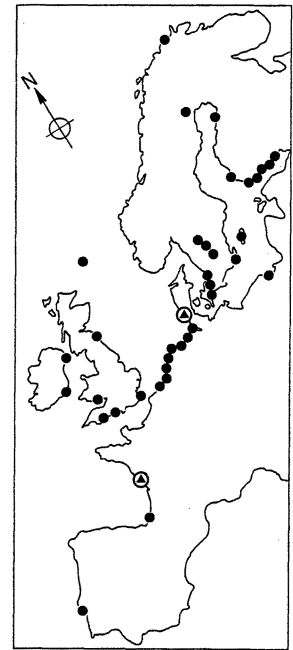
2. Methods

The network of observers contributing to the project is shown in Fig. 1. Sites in Great Britain which were known to be of importance in spring to Nearctic Knots (Prater 1974), were not covered during this project. At most locations, observations on the migration of waders were made throughout the study period April–early June 1979. At three sites (Langebaan Lagoon in S. Africa, Vendée coast in France and Schleswig-Holstein in W. Germany), Knots were captured with mistnets or cannon-nets. Data on bill and wing length were collected to allow subspecific recognition (cf. Dick et al. 1976, Roselaar 1983), and data on weights to yield information on the energy reserves accumulated by the birds before departure from different sites (cf. Davidson 1984). To obtain data on the migratory movements of birds within the spring of 1979, samples of Knots were marked with plumage dyes. At Langebaan Lagoon, 54 adult Knots were dyed yellow orange with picric acid on the undersides, rump and wingbars between February and April. At the Anse de l'Aiguillon, Vendée in France, 200 birds were dyed blue in the same positions, mainly on 12 and 15 May. Observers were requested to scan flocks for colour-marked birds. Spring recoveries of Knots ringed on their wintering grounds have been assembled through the ringers concerned.

A major objective of the study was to establish which areas are of importance to Siberian Knots in spring, and in which periods. Volunteer observers were requested to carry out regular counts in specific areas. Information on the absence of migrating Knots in apparently suitable places was also particularly welcomed. Observations of departing flocks were made at several sites. At departure, Knots become very restless, call characteristically and eventually fly strongly at increasing altitude (pers. obs.). Observers were requested to note size and compass bearing of the departing flocks. Continuous visual observations of passing birds were made at two stations along the coast of the Netherlands and two sites in the Gulf of Finland.

In the period 28 May–21 June 1979, J. Koistinen and A. Harju (Department of Meteorology of the University of Helsinki, Finland) used a 3 cm weather radar (beam width 1.7 degrees, pulse length 0.5 or 3 μ s, pulse power 200 kW) located at Helsinki, Finland, to detect most bird flocks up to 10 km (larger flocks to 25 km). Observations were made by counting the number of flocks within a 20 km radius from Helsinki on the PPI-display (Plan Position Indicator; for explanation of radar, see Eastwood 1967), increasing the elevation angle

Fig. 1. Distribution of observers during the 1979 spring migration project. Not shown is Langebaan Lagoon in S. Africa. Triangles within circles indicate the two main staging sites where Knots were caught in spring 1979 and later.



with two degree intervals. Flight altitude was calculated from distance and elevation angle. Four flock types were discerned on the radar-display on the basis of form, flight-speed and direction, of which one type (moderately strong, at lower altitude towards ENE-E and a higher one towards NE-ENE, both occurring by day and by night), clearly belonged to the 'arctic migrating birds'. Flocks of migrating scoters, geese, and large and small waders could then also be told apart. Correlations with visual observations suggested which migrants were most probably Knots, the decisions being made by Koistinen and Harju after considerable experience. Only flocks which could be identified with some certainty on the radar display, have been included in the analysis.

Latitudes and longitudes of the locations mentioned in the text have been assembled in an Appendix. Dates refer to 1979, unless stated otherwise.

3. The Afro-arctic connection

Fig. 2 shows the approximate breeding and wintering areas of Siberian Knots. The biggest known wintering haunts along the W. African coastline are the Banc d'Arguin in Mauritania (c. 350 000 birds, Altenburg et al. 1983), the Bijagos Archipelago and estuaries in Guinea-Bissau (c. 36 000, Zwarts 1984) and the lagoons in Namibia and S. Africa (c. 10 000, Summers 1977, Whitelaw et al. 1978). (Note however that the entire Gulf of Guinea is as yet unsurveyed for waders.) The above figures suggest a total population size of 400 000–500 000 birds. Biometric information and the exchange of one ringed Knot between Mauritania and S. Africa

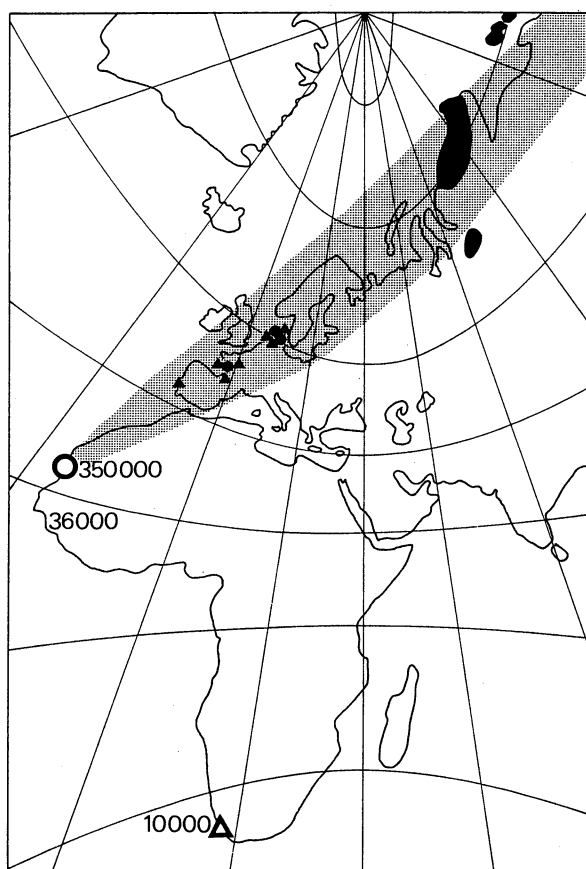


Fig. 2. Seasonal changes in the distribution of Siberian Knots *C. c. canutus*, depicted on a gnomonically projected map of the East Atlantic Flyway (cf. Dick et al. 1976, Engelmoer 1982). Black shows the approximate breeding areas (from Cramp and Simmons 1983, Roselaar 1983). Figures indicate location of the largest known concentrations of Knots in W. Africa. Round symbols indicate the ringing site Banc d'Arguin (open) and the subsequent recoveries from spring (closed), whereas triangles show the same for wintering birds ringed in S. Africa. The shaded band shows the great-circle migration-route postulated by Dick et al. (1976) for Siberian Knot in spring.

indicate that W. African birds belong to the same population (Dick et al. 1976).

Dick et al. (1976) suggested that S. African Knots do not migrate directly via the shortest route to their breeding grounds (13 300 km great circle distance, Fig. 9), but fly via Mauritania and W. Europe (totalling almost 16 000 km, sum of great circle distances). The spring recoveries of Knots ringed in Africa in winter (Fig. 2), support this suggestion. A single S. African-ringed Knot was recaptured at Tejo Estuary, Portugal, in the first week of June. In April–May, three S. African and one Mauritanian ringed Knot were recaptured in W. France, and three S. African and two Mauritanian birds were recaptured in Schleswig-Holstein.

The suggestion that Siberian Knots migrate through western Europe in late spring is also supported by bio-

metric data. Siberian Knots have an average bill length of about 35 mm, while bills of Nearctic birds are 2 mm shorter (Dick et al. 1976). A sample of 12 Knots caught on 12 May in Tejo Estuary, Portugal, had an average bill length of 36.08 mm (range 34–39 mm), clearly indicating Siberian birds. In the Vendée, France, bill lengths on 12 and 15 May also indicated Siberian Knots (average 35.26 mm, SD = 2.02, n = 331). The situation in the Schleswig-Holstein Wadden sea is more complicated because both the Nearctic and the Siberian subspecies occur here in spring (Prokosch 1984). A detailed analysis of biometrics and ringing recoveries by Prokosch (in press) has shown, however, that almost all Knots present before 10 May belong to the Nearctic subspecies, whereas most Knots present after 10 May belong to the Siberian breeding population. This conclusion was based on the following evidence:

- detailed counts in selected areas showed peak numbers of Knots in mid April or in mid May only, or showed two peaks, in April and in May,
- all winter recoveries of Knots ringed in spring in Schleswig-Holstein before 10 May are located in the Wadden Sea or in Great Britain, and all spring and autumn recoveries are located in Great Britain or in Iceland, i.e. implying Nearctic breeding birds (cf. Dick et al. 1976),
- in contrast, all recoveries of Knots caught in spring after 10 May are from western and southern Africa (winter) or western France (spring and autumn) or the Baltic area (autumn), i.e. implying birds breeding in Siberia,
- around 10 May, bill lengths of captured adult Knots increase abruptly from an average 33 mm to an average 35 mm, i.e. a change from typical Nearctic to typical Siberian bill lengths,
- around 10 May average weights of adult Knots show a dramatic drop from about 190 g to about 145 g, implying the departure of heavy birds and the arrival of light birds.

The 1979 colour-dyeing programme yielded only a few resightings, despite extensive observer-coverage. None of the 54 Knots dyed in S. Africa was seen again. Three of the 200 Knots dyed in the Vendée on 12 or 15 May were relocated in the Gulf of Finland, as they passed the Aspskär Bird Observatory on 3 June (one bird) and 6 June (two birds). This indicates that birds staging in the Vendée do indeed migrate in the direction of the Siberian breeding grounds.

Further evidence for the reality of a migration route from W. Africa through western Europe to central Siberia is provided by the compass bearings of departing and passing flocks of Knots (Fig. 3). Knots left the Vendée in a northeasterly direction, as did birds leaving Scharhörn and Sönke-Nissen-Koog in the W. German Wadden Sea. At Amager island near Copenhagen, Denmark, Knots left to the east. Knots passing Schiermon-

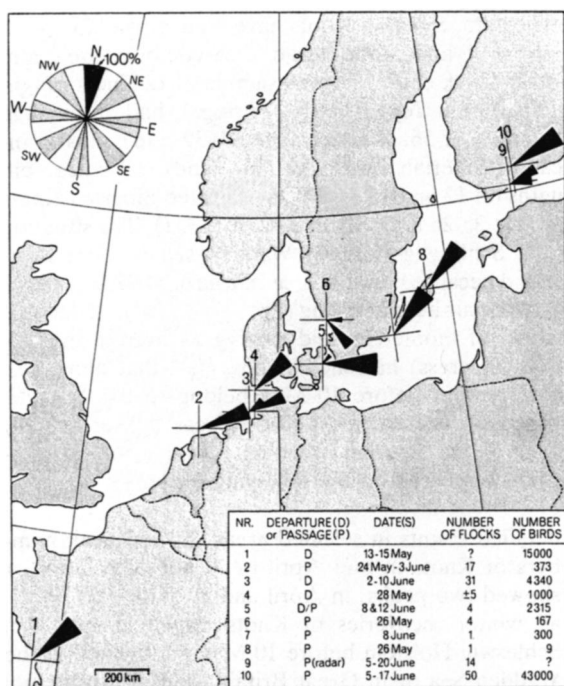


Fig. 3. Flight directions of migrating Knots during the spring of 1979. The percentages of Knots flying in different direction-classes are presented. The inserted table gives details of the observations.

nikoog in the Netherlands and various sites in the Baltic Sea also flew to the northeast, apart from 167 birds at a coastal site just north of Helsingborg in Sweden, which flew to the SE. In the Gulf of Finland birds were flying slightly more in an easterly direction (shown both by radar and visual observations).

4. Occurrence, timing and behaviour on migration

4.1. Timing and locations

A summary of the locations, and the timing of the spring passage of Knots from some locations, is shown in Fig. 4. Details of the data collected during spring 1979 from these and other countries are summarized below.

S. Africa. The departure period was mainly between 14 April and 21 April. Some adults were still present as late as 28 April. The 1979 departure period was both later and more drawn out than in previous years (M. Waltner pers. comm.).

Morocco. No observations were made in 1979, but subsequent work in the March–April periods of 1981 and 1982 (Kersten et al. 1983, van Brederode et al. 1982) indicated a limited passage of hundreds of Knots in early and late April in the Sidi Moussa Estuary, 150 km south of Casablanca.

Portugal. At the lagoon system near Faro, Algarve, southern Portugal, where on average 600 Knots winter, no birds were seen in the period 25–29 April. From 3–7 June 450 were noticed, most probably being summering birds. At the Tejo Es-

tuary near Lisbon (wintering population about 230, Rufino 1984) one Knot was seen on 14 April, 300 Knots on 11 May, 220 on 18 May, while on 29 June a few dozen birds were still present. The latter birds comprised mainly immatures in wing-moult. These observations indicate that at least some hundreds of presumed Siberian Knots stage at the Portuguese coast in May.

France. Knots were counted in the entire Anse de l'Aiguillon from mid April onwards. Fig. 4 shows that there was a rapid build up of numbers to a peak of about 25 000 on 15 May. Flocks, totalling about 15 000 birds, were observed departing in a northeasterly direction on 13, 14 and 15 May. Following this, numbers fell and passage was probably complete soon after 24 May, although further counts were not made. Counts on 11 and 24 April reflect the departure of the Nearctic population, which overwinters in the Vendée (O. Fournier pers. comm.). There is probably little overlap of the two populations in the Vendée. The arrival date of spring migrants in the Vendée in 1979 was at least a week later than in previous years, although departure dates were similar. In the Camargue exceptionally few Knots were seen in spring 1979, about 20 birds. Numbers fluctuate very much from year to year, maximum counts ranging from 26 to 1 100 birds, the major passage period being during the first week in May.

Belgium. There are no important feeding areas for Knot along the Belgian coastline. Large numbers of Knots have been observed in previous years migrating at sea, but quantitative data are not available. Counts of small numbers of resting Knots near Oostende in previous years show the spring peak during May.

Britain. Counts were made at Sandwich Bay in SE England on an almost daily basis. Very few Knots were observed and there was no pattern discernable. This contrasts to the position in autumn when Knots, probably mainly juveniles of the Siberian population, are more numerous. A series of counts on Whalsay, Shetland Islands (Fig. 4) may indicate passage of a few birds in the second half of May. Zero counts were made at Poole Harbour on the south coast of England and in Glamorgan, south Wales. All these are 'marginal' areas for wintering Knot. The major estuaries along the east coast were not counted due to the problems of separating small numbers of Siberian passage birds from Knots of the Nearctic population.

The Netherlands. About 2 000 Knots were counted in the Oosterschelde part of the Delta area in mid May (Meininger et al. 1984). However, counts around 15 May 1980 indicated the presence of 10 000 Knots in the Westerschelde (not surveyed in 1979) and another 1 000 birds in the rest of the Delta area. Daily observations of migrating birds along the Dutch North Sea coast indicated heavy passage of Knots in early June (Fig. 4), although no counts were made during the period (around 20 May) in which most Knots normally pass. The occurrence close to the shore is strongly subject to wind conditions (Camp-huysen and van Dijk 1983). Counts on the little island of Griend in the Dutch Wadden Sea showed a declining Knot population from 6 000 birds on 23 April to 500 on 17 May and zero on 20 May, probably Nearctic birds. On 21 May 2 900 Knots were suddenly present (900 on 23 May, 100 on 27 May) indicating a rapid passage through this area. Seventy km further east, a set of counts was made on the island of Schiermon-nikoog on a daily basis. Zero counts were made from 13 April to 23 May. Flocks of 10 to 125 Knots were observed resting or migrating in a ENE direction on most days from 24 May to 4 June, when observations ceased. No Knots were seen on the small islands Rottumeroog and Rottumerplaat. The Dutch Wadden Sea is of far less importance to its main Nearctic Knot population during spring than it is in autumn (Smit and Wolff 1981). The passage of Siberian Knots during 1979 was considered to be about a week later than in previous years.

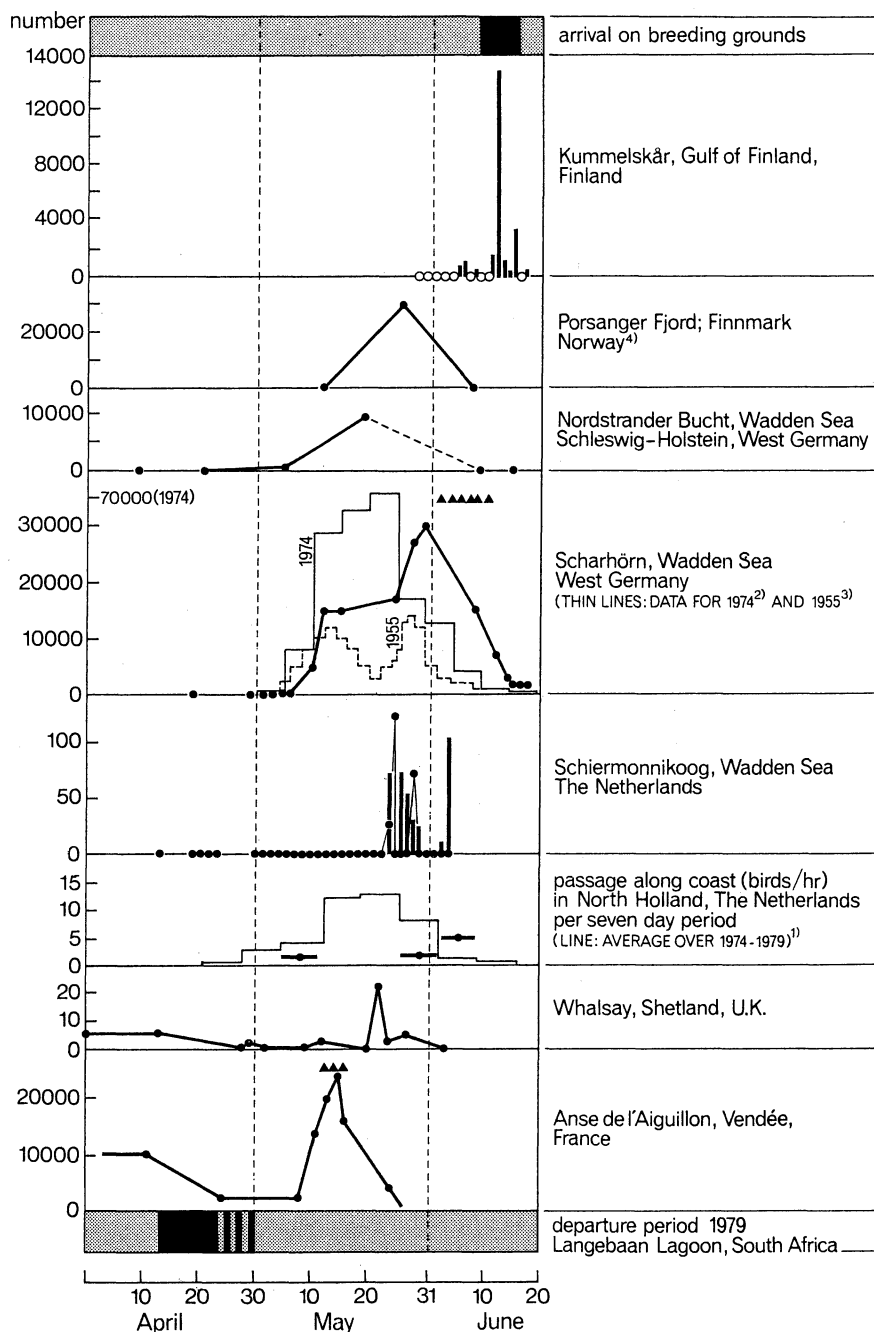


Fig. 4. Occurrence and timing of Siberian Knots at different sites along the migratory flyway during spring 1979. Dots indicate numbers of birds on the ground, bars numbers of passage birds. Triangles indicate dates when major departures were observed. For some sites additional data for years other than 1979 are given. Sources other than from project: (1) Camphuysen and van Dijk 1983; (2) Comes and Goethe 1978; (3) Temme 1967; (4) Berg 1979 in Håland and Kålås 1980.

W. Germany. On the island of Scharhörn in the Elbe estuary practically no Knot appear, except on migration. Numbers built up rapidly to about 15 000 birds between 5 and 12 May. There was a further increase to 30 000 on 30 May (Fig. 4). Flocks were observed departing from Scharhörn between 2 and 10 June (see Fig. 3), which coincided with a rapid fall in numbers to only 200–500 by 16 June. The 1979 counts reflect a similar pattern to the 1974 and 1978 counts, although there were less marked peaks at the end of May in both 1974 (shown only, Fig. 4) and 1978 (omitted for reasons of clarity). Counts made in 1955 suggested a marked double peak in spring numbers

(Temme 1967, Fig. 4). Further north in W. Germany, counts were made over the whole of the Schleswig-Holstein coast by air and, at certain areas on the coastline, on a regular basis on the ground. The following approximate totals of Knot were counted over the Schleswig-Holstein coast in 1979: 48 000 on 25 March, 139 000 on 22 April and 253 200 on 6 May. Huge Knot flocks were seen in the north-western part of the Wadden Sea of Nordfriesland (around the islands of Sylt, Amrum, Föhr and Langeness) in April and the beginning of May, but hardly any bird was present there in the second half of May (see also Fig. 8). Counts in the Nordstrander Bucht showed a different

picture: nearly 10 000 Knots were present on 20 May and very few on 6 May and 10 June (none in March and April, Fig. 4). Five smaller study areas in the Nordstrander Bucht showed peak numbers between 20 and 31 May. Counts in recent years suggest that a total of at least 200 000 (Siberian) Knots occur in the latter half of May in the W. German Wadden Sea.

Denmark. The part of the Wadden Sea north of the Danish border has been shown to be of little importance in spring to Knot, in comparison with the W. German part (Meltøfte 1969 and pers. comm.). On Amager island, near Copenhagen, three flocks of 500, 500 and 1 000 Knot were seen departing on migration due east on 8 June. On 12 June a flock of 315 Knots, all in summer plumage, passed the island of Saltholm, also near Copenhagen, in a northeasterly direction.

Norway. In the Porsanger fjord, Finnmark, N. Norway, Berg (1979) counted 30 000 Knots on 26 May with zero counts on 2 May and 8 June. These data fit with the observations of Randa (1976) who found up to 2 500 Knots in the Finnmark area in the last week of May 1970–1972. Håland and Kålås (1980) suggest that these concentrations of Knot belong to the Siberian breeding population, but did not substantiate this by biometric or other data. In contrary, as a result of biometric studies in May 1985, Davidson et al. (1986) were able to show that these Knots belong to the Nearctic breeding population.

Sweden. Eleven observations of between one and four Knots were made at scattered locations on the following dates: 24, 25 March, 1 April, 16, 20, 22, 23, 25 May, 3, 6, 12 June. Four of these were at inland sites, and the three records prior to 16 May were all in the Skåne district, close to Denmark. In addition, 28 Knot were seen in Skåne on 20 May, 300 Knot were seen flying NE at Ottenby, Öland on 8 June and 9 were seen on the island of Gotland on 26 May, flying in a northeasterly direction. Knots do not rest or feed on the Swedish coasts in spring, and are only seen irregularly, particularly in bad weather. In previous years flocks have been seen on Öland in spring: 600 on 9 June 1969, 120 on 12 June 1969, 1 000 on 30 May 1970, 150 on 6 June 1971, 100 on 28 May 1976, 370 on 29 May 1976, 160 on 30 May 1976 and 55 on 25 May 1977.

Poland. Observations were made on the small estuaries of the Rivers Vistula and Reda. Two Knots in breeding plumage were seen on 7 June at the Vistula. Knot occur only in small numbers in spring and autumn on the Polish coastline.

Finland. Counts were made on a daily basis at Tauvo and Yyteri, in the Gulf of Bothnia. No Knot were seen at Tauvo from mid April until 15 June. At Yyteri only two individuals were seen on 3 and 5 June in spite of daily counts in May and June. In previous springs also very few Knot have been seen at Yyteri, with a maximum of 5 to 10 observations per year. In the Gulf of Finland, observations were made on a daily basis at Aspskär and Kummelskär Bird Observatories and also at Hanko, Rönnskär and Kukio. Passage of hundreds of Knots were reported from the latter three sites in the period 1–13 June. (Some birds were seen earlier: three Knots on 15 May at Hanko and 12 on 25 May near Kukio.) At Aspskär, in the mouth of the Gulf of Finland, no passage of Knot was seen from 30 April to 2 June and from 7–10 June. Passage of about 1 500 birds in 12 flocks was observed from 3–6 June. At Kummelskär, a little rocky islet about 40 km SE of Helsinki, continuous watches were made from 28 May to 17 June, and the passage of Knot at this site is shown in Fig. 4. From 3–17 June at least 23 000 Knots passed here, with peak counts on 12 June. In the same period, radar observations at Helsinki revealed the passage of at least 14 probable Knot flocks in the period 5–20 June, eight of which were noticed on 6–8 June. The flocks which were observed by radar certainly escaped the attention of the visual observers, by flying too high (see below). If we assume that the migrating flocks noticed on the radar have the

same average size as the lower flying flocks at Kummelskär (i.e. 800 birds), then $23\,000 + (14 \times 800) = 34\,000$ Knots can be estimated to have passed through the Gulf of Finland in June 1979. However, a big proportion of 'large unidentified waders' seen on passage by the observers at Kummelskär and of the 'arctic flocks' seen on the radar display, were most probably Knots, so that we may add at least 30 000 birds. This results in a minimum estimate of a passage of 60 000–70 000 Knots in spring 1979. It should be noted that Knots never stop to feed or rest on the Finnish coast in great numbers and also, that the numbers seen are very variable from year to year depending on the weather conditions. It is clear though, that the Gulf of Finland is a major migratory route for Siberian Knots on their way from Schleswig-Holstein to the central Siberian tundra.

Soviet Union. Although no data were collected in spring 1979, some observations from the north Russian tundra have been communicated by P. S. Tomkovich and V. K. Ryabitsev. There are some records of concentrations of Knots on the western shore of Kanin Peninsula in early June. Near Nes, on south Kanin Peninsula, individual Knots and several flocks of 3–60 birds were recorded in the period 17–21 June 1969 on a wet tundra near the sea coast, but this appears to be rather exceptional. Further eastwards there are no records of concentrations of Knots up to Taymir Peninsula. No Knots were ever noticed on Yamal Peninsula during a research project in the period 1970–1984. On Taymir Peninsula, the arrival of first Knots was recorded on 9 June 1982 near Dikson and on 14 June in Lenivaya River mouth. No visible migration ever appeared in these two seasons. Near the mouth of Uboinaya River (65 km eastwards from Dikson) in 1984 migration of Knots occurred from 8 June onwards (some single singing birds and one transit flock of 12 birds). More intensive migration took place on 10 June 1984 with seven flocks of 6–54 birds (totalling 154) passing in five afternoon hours in eastward direction along the seashore. Later in June only a few single birds and pairs were seen here, and extremely few birds actually bred.

4.2. Summary of the migration

The following pattern of occurrence and timing of Siberian Knots migrating to their breeding grounds in spring emerges. Knots leave S. Africa in the second half of April, probably migrating northwestwards to Guinea-Bissau and/or Mauritania. Knots arrive around 10 May in the Tejo Estuary in Portugal, the Vendée coast in France, the Westerschelde in the Netherlands and especially the W. German Wadden Sea, suggesting a departure of Knots from W. Africa in the first week of May. Knots rest only one or two weeks in Portugal and France, probably then flying onwards to the Schleswig-Holstein Wadden Sea. In Schleswig-Holstein at least 200 000 Siberian Knots are present for three or four weeks with all birds leaving in the first week of June. The departure from W. Germany is immediately followed by records of Knot passage through the Baltic Sea in early June and very heavy (concentrated) passage through the Gulf of Finland in the second and third week of June. Although some flocks may sometimes stop in the White Sea area on Kanin Peninsula, most birds probably fly straight on to Taymir Peninsula and other breeding grounds, where arrivals are recorded in the same period as the passage through the Gulf of Finland.

The data therefore suggest that the majority of Knots leaving from W. Africa use only one stopover-site (the W. German Wadden Sea) on their migration to central Siberia. A minority of the birds seems to alight at Tejo Estuary, Vendée coast, Westerschelde and the Dutch Wadden Sea.

4.3. Diurnal pattern in migration intensity

Some data have been collected on diurnal variations in the timing of departure and passage of Knots. Along the Dutch North Sea coast, Knots passed throughout the daylight period with no apparent peaks, whereas on Schiermonnikoog birds also passed throughout the day but were only seen around high tide. At Scharhörn all 4500 birds left in the late afternoon between 17.50 and 20.05 hours (local time). At Amager, Denmark, flocks left in the morning at 10.30 and another passed Salt-holm at about 14 hours. At Kummelskär in the Gulf of Finland, heaviest passage occurred in the late afternoon: 16–22 hours (76.6% of 23 260 birds), with less mi-holm at about 14 hours. At Kummelskär in the Gulf of Finland, heaviest passage occurred in the late afternoon: 16–22 hours (76.6% of 23 260 birds), with less migration in the periods 22–04 (5.6%), 04–10 (11.4%) and 10–16 hours (6.4%). The Helsinki radar noticed most flocks at night (22–04 hours: 50% of 14 flocks) and fewer in the periods 04–10 (36%) and 10–16 hours (14%). It is striking that no birds were seen by radar in the late afternoon when passage was heaviest along the nearby bird observatory, suggesting a diurnal variation in flight altitudes.

4.4. Flight altitudes

Flocks of Knots passing visual observers in the Netherlands were always flying low over the water (< 10 m). In Schleswig-Holstein, mixed flocks of departing Knots, Bar-tailed Godwits *Limosa lapponica* and Grey Plovers *Pluvialis squatarola* circled to such altitudes that they 'vanished in the sky'. Data on flight altitudes were collected by radar and visual observers near Helsinki in Finland (Fig. 5). Most Knots which were noticed by the observers passed at estimated heights of 100–500 m, but the radar observations showed that flight altitudes can actually be as much as 3 km. Most flocks passed the Helsinki-radar at heights between 1 and 1.5 km.

5. Weights during migration

Weights are available from S. Africa, Portugal, France and W. Germany and are partly summarized in Fig. 6. In spring 1979 only 13 Siberian Knots were captured in Schleswig-Holstein, but over the period 1979–1983 larger samples were obtained. Therefore all available information on weights of adult Siberian Knots at this site has been used (Fig. 7). In Fig. 6 the weight distributions are shown for the earliest and latest catching days

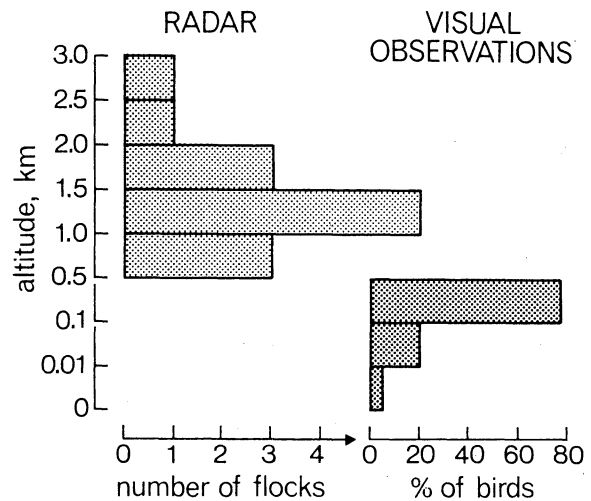


Fig. 5. Flight altitudes of Knots through the Gulf of Finland in May 1979 as determined by radar observations by the weather radar at Helsinki and visual observations of passage birds at Kummelskär Bird Observatory. Sum of (positively identified) Knots at Kummelskär was 22 980 birds.

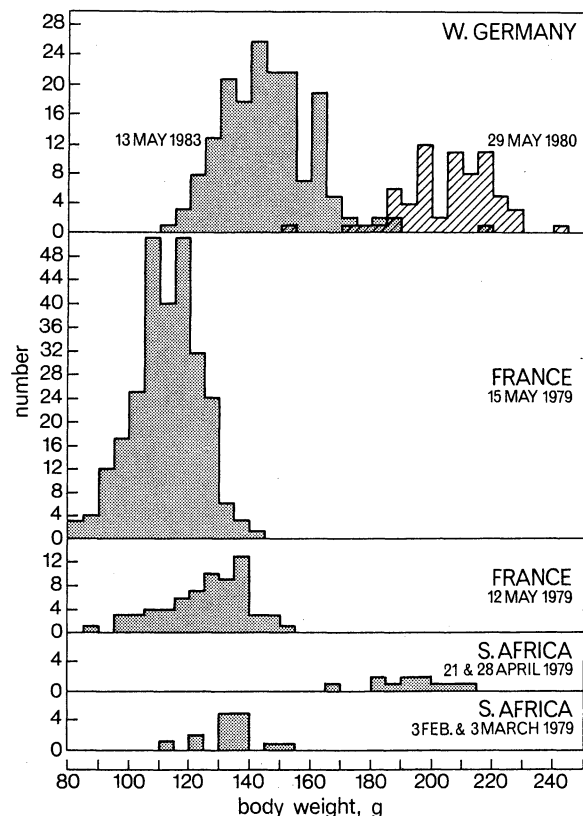


Fig. 6. Body weight distributions of adult Siberian Knots at three sites along the migratory flyway in spring 1979.

of Siberian Knots in W. Germany regardless of year of collection. In South Africa, the mean weight of catches on 21 and 28 April was 188 g. Previous years' data have shown an increase in weights from a 'summering' (i.e. northern winter) weight of about 130 g to a mean of about 190 g at departure (Summers and Waltner 1979). Bearing in mind that it is probably the top quartile of individuals in such weight distributions which have achieved departure weight, 210 g may be a normal departure weight. A sample of Knots caught at Tejo Estuary, Portugal on 12 May 1979 (not shown in Fig. 6), had an average weight of 123 g (range 103 to 164 g). In the Vendée, mean weights on 12 and 15 May were 126.1 and 113.5 respectively. These are very low weights indeed, some birds weighing as little as 84 g. Fat-free weights of Siberian Knots in Morocco in spring are about 110–115 g (pers. obs.). Minimum survival weight of juvenile Knot found in Mauritania was about 65 g

(Dick and Pienkowski 1979). Arrival weights in the Vendée may therefore represent depletion not only of fat reserves, but also of other body reserves, such as protein. It is interesting to note that the difference in mean weights between 12 and 15 May is partly due to the departure of birds weighing more than 130 g (Fig. 6). This period corresponds with observed departures from the Vendée (see above). In the Schleswig-Holstein Wadden Sea the population weights seem to increase steadily throughout the staging period (Fig. 7). The earliest sample on 13 May 1983 had an average weight of 144 g and the latest sample on 29 May 1980 an average weight of 206 g. If only the top quartile of birds in this latter weight distribution would be ready to leave (main departure 3–7 days later, see above), departure weights would be about 225 g. The increase from 144 g on 13 May to 206 g on 29 May suggest an average weight increase of 3.9 g d^{-1} for an 'average' Siberian Knot. This is obviously a minimum, because the arrival of light birds and the departure of the heaviest birds will depress the apparent increase in weight as measured by mean weights of birds present at a site. It is suggestive that three individual Knots, recaptured on different dates in May (though in different seasons), showed weight increases of 4.0, 4.5 and 5.0 g d^{-1} . This is also more than the 3 g d^{-1} weight increase originally assumed by Dick (1979) and given by Prater and Wilson (1972) for Nearctic Knots in Britain and Iceland.

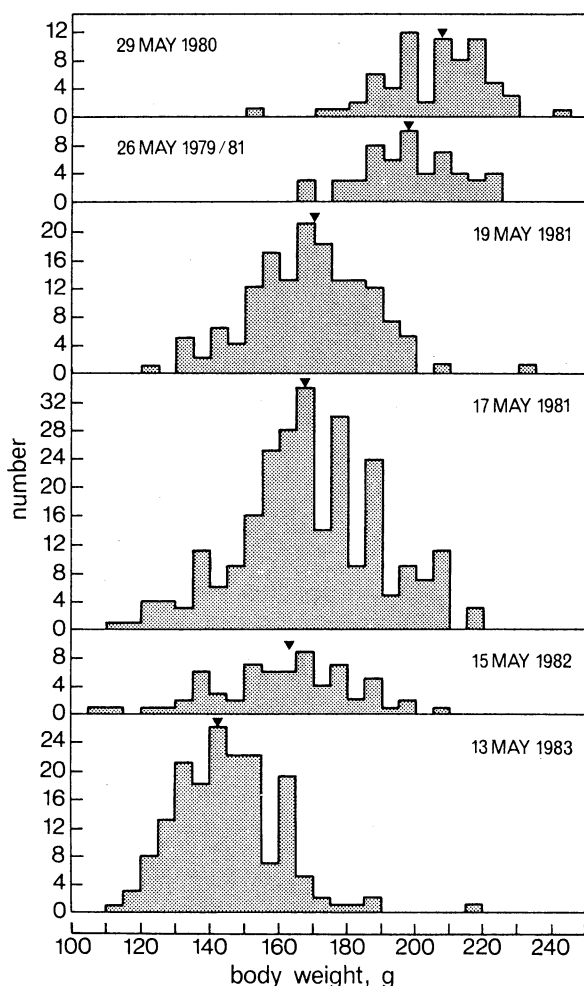


Fig. 7. Body weight distributions of adult Siberian Knots in Schleswig-Holstein at different dates in May in various years. Triangles indicate average weights for each date.

6. Discussion

6.1. Temporal and spatial segregation of Siberian and Nearctic Knots

The breeding grounds of Siberian Knots and Nearctic Knots are well separated. However, at the autumnal staging areas the pattern seems to be different. From mid July onwards, Nearctic Knots return from the breeding grounds to their main moulting areas in the Dutch and German Wadden Sea and the Wash, U.K. (Prater 1974, Pienkowski *im Cramp* and Simmons 1983). After moult, there is some movement to the west, and the largest wintering concentrations are found on the British Isles. Siberian Knots arrive somewhat later than Nearctic Knots in the Wadden Sea and Wash (mainly the end of July and the beginning of August, *Cramp* and Simmons 1983) and move on rapidly to the moulting and wintering areas in W. Africa. On the Banc d'Arguin they begin to arrive in early September (Dick *et al.* 1976). Boere *et al.* (in press) show that in August and September both breeding populations occur simultaneously in the Dutch Wadden Sea. On the wintering areas, segregation between Siberian and Nearctic Knots is believed to be complete again (Dick *et al.* 1976).

During spring migration separation remains almost complete, as was shown above: Nearctic Knots have left the wintering and spring staging areas in France and the Dutch and W. German Wadden Sea before the Siberian

birds arrive there in early May. Both in spring and in autumn, the Nearctic birds seem to be somewhat earlier in schedule, which may be related to different climatic features of their arctic breeding areas. Not only do the two Knot populations seem to be temporally segregated, but to some extent they appear also to be spatially segregated where using the same general spring staging area. Fig. 8 shows how 'early' (presumed Nearctic) and 'late' (presumed Siberian) Knots are distributed throughout the Schleswig-Holstein Wadden Sea in April and May. The 'late' Knots tend to use only the southern half of the area and not the northern half where biggest concentrations of Knot occur earlier. Hence, only in early autumn do the two subspecies of Knot occur in large numbers in the same area at the same time.

6.2. Energy acquisition and the timing of migration

An integration of the data on timing and body weights of Siberian Knots during spring migration, collected during this co-operative study, may lead us to an appraisal of the energetics of the migration strategy of this long distant migrant. The problem can be attacked from many sides and, with the current level of knowledge, many assumptions have still to be made. We have chosen to present a simple graphical model of the changes in body weight (Fig. 9), which integrates the data on number and position of staging sites, probable migration distances, departure and arrival times, and body weights at arrival and departure. Dates of departure or

arrival at various sites have been fixed as realistically as possible as follows: departure from S. Africa on 17 April, arrival in the Vendée, France and in the Wadden Sea, W. Germany on 8 May, departure from France on 14 May and departure from the W. German Wadden Sea on 4 June. Flight distances (Fig. 9) and an assumption on the flight speed of Knots as 80 km h^{-1} allow us to calculate the arrival and departure dates at the Banc d'Arguin, Mauritania, the 'postulated' staging site between S. Africa and W. Europe. To simplify this picture, we do not discuss the possible role of coastal Guinea-Bissau as a staging site. For the purposes of discussion, some further assumptions are made as follows:

- migration follows great circle routes,
- wind-free conditions occur during migratory flights,
- variations in body weight are entirely due to variations in fat load,
- the flight range formula of Davidson (1984) is essentially realistic (i.e. flight range (km) = $95.447 \times \text{flight speed } (80 \text{ km h}^{-1}) \times ((\text{weight at start, g})^{0.302} - (\text{weight at end of flight, g})^{0.302})$),
- a rate of weight increase of 3 g d^{-1} for the Banc d'Arguin (the same as for S. Africa) and of 4 g d^{-1} for France and W. Germany.

It is now possible to ask whether a Knot, with the above constraints on timing and fattening rates, could theoretically make the journey from S. Africa, via Mauritania and W. Europe to the arctic breeding grounds; in

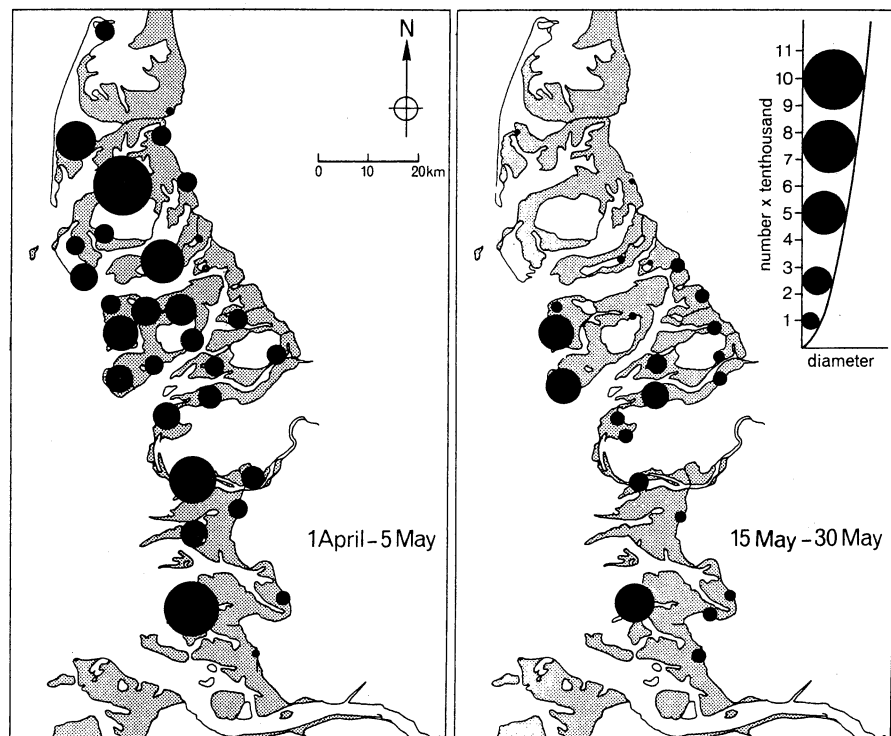


Fig. 8. Spring distribution patterns of 'early' and presumed Nearctic Knots (left) and 'late' and presumed Siberian Knots (right) in the Wadden Sea of Schleswig-Holstein, W. Germany. Combined data of counts in several spring seasons (1979–1983).

other words, are our theories and assumptions compatible with observations?

Fig. 9 shows that a Knot starting from S. Africa will have depleted its fat reserves by the time it arrives in Mauritania. If this bird were unable to fatten at a rate of more than 3 g d^{-1} , it would not be able to deposit sufficient fat to migrate in one flight to W. Germany, but instead would have to stop in France, already with more than depleted fat reserves. (Note that Fig. 9 also shows that a direct flight from S. Africa to France would be impossible.) Birds arriving at the same time in W. Germany did not have the very low weights recorded in France (see Fig. 6), but weighed about 120 g. For these Knots, a departure weight of 182 g is predicted for the Banc d'Arguin in Mauritania. Birds from S. Africa would have to deposit fat at 5 g d^{-1} after arrival in Mauritania to reach W. Germany in the same body condition. If departure dates were indeed fixed on e.g. 4 June (a short breeding season and a premium on early arrival, Pienkowski et al. 1985, Alerstam and Högstedt 1985), and if fattening rates were limited to 4 g d^{-1} in W. Germany, then the group of Knots alighting in France would (have to) start with lower departure weights, and hence arrive in poorer condition (i.e. lower fat levels) on the central Siberian breeding grounds than the early arriving birds in W. Germany. The latter birds may be the wintering birds of the Banc d'Arguin.

Obviously, different individuals will travel with different time schedules and weight patterns. However, from Fig. 9 we may predict that: (1) spring departure weights of Knots from the Banc d'Arguin are on aver-

age lower than those for S. Africa and W. Germany (and thus not close to 210 g as assumed by Dick 1979); (2) S. African wintering birds appear to fall behind the optimum schedule of fattening because of the extra distance flown, and are overrepresented in the groups stopping over in Portugal, France and SW Netherlands, before arriving in the W. German Wadden Sea; (3) birds stopping between Mauritania and W. Germany arrive in a poorer condition on the breeding areas than birds which do not so, and would therefore be expected to have a lower breeding success or lower survival; (4) the majority of Knots arriving in central Siberia have not depleted their fat reserves, and could be expected to carry 40 g of fat reserves on arrival.

The ratio between recoveries of S. African and Mauritanian ringed birds tends to be somewhat higher in Portugal (1:0, Fig. 2) and France (3:1) compared with W. Germany (3:2), supporting the second prediction. The three S. African ringed Knots which were recaptured in W. Germany in May, were of relatively low weight (8, 19 and 22% below the average). S. African Knots could, in theory, 'solve' the problem of timing and fattening if the amount of fat used during the flight to Mauritania is actually lower than predicted (e.g. with the use of tail winds during the migratory flight), if rates of fat deposition on the Banc d'Arguin are not limited to 3 g d^{-1} , or if they have more time available on the Banc d'Arguin. The same is true for the Vendée birds arriving in W. Germany. If they were able to gain weight at rates higher than 4 g d^{-1} or could depart later than 4 June, they would arrive in a 'good' body condi-

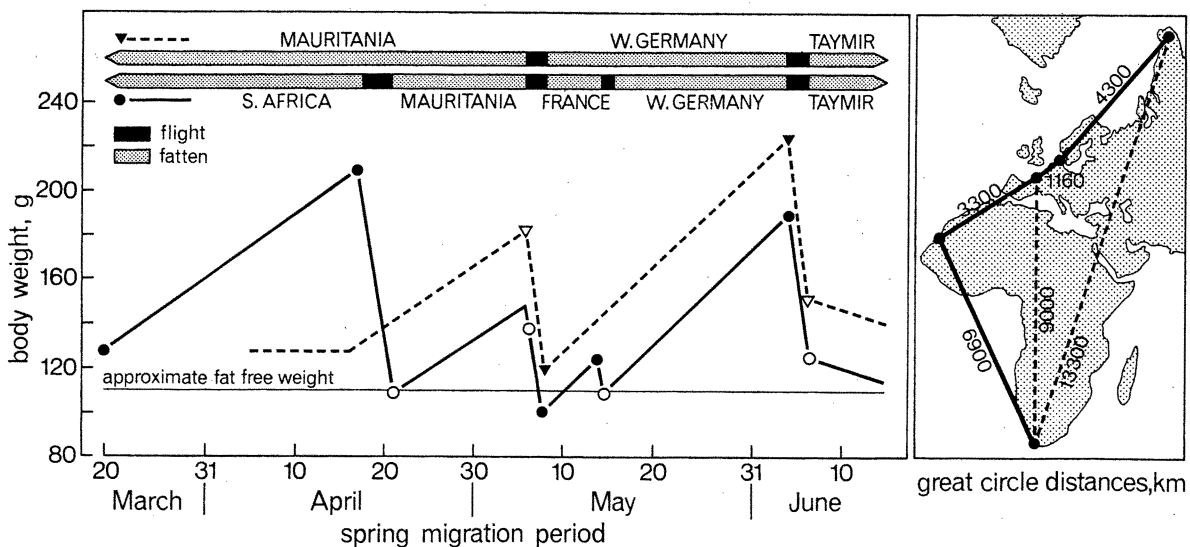


Fig. 9. Graphical and schematical model of changes in body weight of an 'average' Siberian Knot migrating northwards in spring on a fixed time schedule. See text for assumptions and further explanation. Examples are shown of birds from either the S. African (dots) or the Mauritanian (triangles) wintering areas and stopping (or not) at the Vendée coast in France and in Schleswig-Holstein, W. Germany. Closed symbols show 'known' body weights at arrival and departure, computed as the averages of the lower or upper quartiles of the weight distributions (Fig. 6) at first and last sampling dates. Open symbols are weights on arrival and departure subsequently estimated by solving Davidson's (1984) flight range formula for the appropriate great circle distance (see map at right) and for the 'known' departure or arrival weight.

tion on the breeding grounds. Nevertheless, the data from 1979 seem to indicate that at least the French group of Knots were energetically worse off and behind schedule compared with birds arriving early in W. Germany.

From a purely energetic point of view, making more and smaller migratory 'hops' is cheaper than one long flight, because the more fat that is loaded, the more it costs to transport this fat. The 'first' fat that is deposited thus yields the most in terms of distances flown. Nevertheless, Knots seem to be a species adapted for very long flights (see also Morrison et al. 1980, Morrison 1984, Davidson 1984). The minority of birds which make shorter flights and more stops do so because they seem to be the birds which, for whatever reason, have problems in making the long journeys.

We hope to have shown that a large-scale international effort to study the migration of one species, can be scientifically rewarding. Data from locations which in isolation have little value, can be interpreted to yield an overall conclusion with international co-operation. Further work, with emphasis on the role of the tidal areas in Guinea-Bissau and the Banc d'Arguin in spring, would add greatly to the understanding of the spring migration strategy of Siberian Knots. The dependence on only a few coastal sites during migration, makes this pre-eminent migrant species particularly vulnerable, and it therefore certainly deserves further attention.

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Appendix. Co-ordinates of locations mentioned in the text

Amager	55°45'N, 12°38'E	Kummelskär	60°10'N, 25°50'E	Sandwich Bay	51°18'N, 01°25'E
Amrum	54°65'N, 08°37'E	Langebaan Lagoon	30°10'S, 18°05'E	Scharhörn	53°57'N, 08°25'E
Anse de l'Aiguillon	46°15'N, 01°12'W	Langeness	54°65'N, 08°56'E	Schiermonnikoog	53°29'N, 06°18'E
Aspskär	60°15'N, 26°24'E	Lenivaya River		Sidi Moussa Estuary	31°00'N, 08°47'W
Camargue	43°30'N, 04°30'E	mouth	75°20'N, 89°06'E	Skåne	55°30'N, 13°30'E
Casablanca	31°36'N, 07°35'W	Nes	66°40'N, 44°47'E	Sönke-Nissen-Koog	54°40'N, 08°45'E
Copenhagen	55°52'N, 12°31'E	Nordstrander Bucht	54°32'N, 08°45'E	Sylt	54°89'N, 08°37'E
Dikson	73°28'N, 80°35'E	Öland	56°30'N, 16°30'E	Tauvo	64°50'N, 24°35'E
Faro	37°00'N, 08°05'W	Oostende	51°12'N, 02°54'E	Tejo Estuary	38°40'N, 09°05'W
Föhr	54°72'N, 08°56'E	Ottenby	56°16'N, 16°31'E	Uboinaya River	
Glamorgan	51°30'N, 03°30'W	Poole Harbour	50°43'N, 01°59'W	mouth	73°30'N, 82°16'E
Gotland	57°30'N, 19°00'E	Porsanger fjord	70°10'N, 24°50'E	Vistula River	
Griend	53°15'N, 05°15'E	Reda River mouth	54°15'N, 15°00'E	mouth	54°20'N, 19°00'E
Hanko	59°40'N, 23°00'E	Rönnskär	59°50'N, 24°23'E	Wash	52°90'N, 00°35'E
Helsingborg	56°03'N, 12°41'E	Rottumeroog	53°32'N, 06°35'E	Westerschelde	51°22'N, 03°45'E
Helsinki	60°06'N, 24°52'E	Rottumerplaat	53°32'N, 06°29'E	Whalsay	60°21'N, 01°25'W
Kanin Peninsula	67°30'N, 45°00'E	Saltholm	55°50'N, 12°44'E	Yyteri	61°30'N, 21°40'E
Kukio	60°40'N, 28°00'E				